
The Value of Biodiversity in Reserve Selection: Representation, Species Weighting, and Benefit Functions

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Abstract: *The limited availability of resources for conservation has led to the development of many quantitative methods for selecting reserves that aim to maximize the biodiversity value of reserve networks. In published analyses, species are often considered equal, although some are in much greater need of protection than others. Furthermore, representation is usually treated as a threshold: a species is either represented or not, but varying levels of representation over or under a given target level are not valued differently. We propose that a higher representation level should also have higher value. We introduce a framework for reserve selection that includes species weights and benefit functions for under- and overrepresentation (number of locations for each species). We applied the method to conservation planning for herb-rich forests in southern Finland. Our use of benefit functions and weighting changed the identity of about 50% of the selected sites at different funding levels and improved the representation of rare and threatened species. We also identified a small area of additional land that would substantially enhance the existing reserve network. We suggest that benefit functions and species weighting should be considered as standard options in reserve-selection applications.*

Key Words: complementarity, maximum species coverage, overrepresentation of species, site-selection algorithm, underrepresentation of species

El Valor de la Biodiversidad en la Selección de Reservas: Representación, Ponderación de Especies y Funciones de Beneficio

Resumen: *La limitada disponibilidad de recursos para la conservación ha llevado al desarrollo de muchos métodos cualitativos para la selección de reservas que tienen como meta maximizar el valor de la biodiversidad de las redes de reservas. En los análisis publicados, las especies son consideradas iguales a menudo, a pesar del hecho de que algunas tienen mayor necesidad de protección que otras. Más aún, la representación generalmente es tratada como umbral: una especie es representada o no, pero los niveles de representación por arriba o por debajo de un nivel determinado no son valorados diferentemente. Proponemos que un mayor nivel de representación también debería tener un mayor valor. Introducimos un marco de referencia para la selección de reservas que incluye la ponderación de especies y funciones de beneficio para la falta de- y la sobre-representación (número de localidades para cada especie). Aplicamos el método a la planificación de la conservación de bosques ricos en hierbas del sur de Finlandia. Nuestro uso de las funciones de beneficio y ponderaciones cambió la identidad de alrededor de 50% de los sitios seleccionados en diferentes niveles de financiamiento y mejoró la representación de especies raras y amenazadas. También identificamos una pequeña área de terreno adicional que daría realce sustancial a la actual red de reservas. Sugerimos que se*

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considere a las funciones de beneficio y a la ponderación de especies como opciones estándar en la selección de reservas.

Palabras Clave: algoritmo para la selección de sitios, complementariedad, falta de representación de especies, máxima cobertura de especies, sobre-representación de especies

Introduction

Computational techniques, often called site-selection algorithms or reserve selection methods, have been developed to optimize allocation of conservation resources (Pressey 1999; Margules & Pressey 2000; Cabeza et al. 2004; Williams et al. 2004 for reviews). These algorithms operate based on the concept of complementarity (Vane-Wright et al. 1991), in which individual reserves contain different sets of biodiversity features (often species). Use of complementarity induces the selection of sites that cover all biodiversity features evenly and without much redundancy, thereby promoting efficient use of conservation resources. Here we concentrated on issues that have received little attention in the context of complementarity-based reserve-selection algorithms: weighting of species and valuing of different levels of species representation.

It has long been recognized that species are not of equal value and should be prioritized (weighted) for conservation purposes (e.g., Vane-Wright et al. 1991). The earliest reserve-selection methods scored sites by weighting their biological (and other) features. The different attributes were then combined into a site-specific score (Margules & Usher 1981), and sites with the highest scores were selected. A serious shortcoming of the scoring method is that it ignores complementarity, potentially leading to inefficient reserve structures with high redundancy for some biological features and inadequate coverage for others (Williams et al. 2004).

Whereas scoring relies on weighting different features of sites, weights have mostly been overlooked by complementarity-based reserve-selection methods, probably partly because of difficulties in defining the weights and partly for computational reasons. Complementarity-based reserve selection methods are commonly variants of the minimum set (Pressey et al. 1997) and maximum coverage approaches (Church et al. 1996). The minimum set approach aims to cover a given target level of representation of every species for a minimum cost. The maximum coverage approach assumes that not everything can be protected, and the aim is to cover as many of the species as possible for a fixed budget constraint. Several authors have suggested the possibility of weighting species in maximum-coverage reserve selection, based on taxonomic or genetic distinctiveness, rarity, endemism, or economic value (e.g., Church et al. 1996; Arthur et al. 2002; Camm et al. 2002; Önal 2003), but weights were

not actually used in any of these applications. An indirect weighting can be introduced in the context of the minimum set formulation by varying species-specific representation targets.

In these studies species value in a reserve network is typically considered a 0/1 step function, where a species is covered when its representation level exceeds a given target threshold; otherwise, the value of the representation for the species is zero. The problem here is that a species may be present in a proposed reserve network, but if it is slightly below the threshold it will be counted as absent. Similarly, overrepresentation enhances the probability of persistence of any species, but with the step function all potential reserve networks receive the same value regardless of how much the representation threshold is exceeded for different species.

We investigated a generalized variant of the maximum coverage approach, in which the aim was to incorporate as much value as possible into a reserve network, given limited funding. We weighted species based on their regional and national rarity and taxonomic distinctiveness. Importantly, we also assumed that the value of a species in the reserve network is an increasing function of its representation, and we gave value to over- and underrepresentation with respect to a given reference (target) level. The proposed methodology is demonstrated by applying it to conservation planning for herb-rich forests in southern Finland.

Methods

Reserve-Selection Formulation

We investigated a reserve-selection formulation in which the objective was to maximize the value of biodiversity in the selected reserve network:

$$\begin{aligned} \max F(\mathbf{X}) &= \sum_j V_j [R_j(\mathbf{X}), T_j, w_j], \\ \text{given that } \sum_i c_i x_i &< C. \end{aligned} \quad (1)$$

Here the solution is given by a selection vector $\mathbf{X} = \{x_i\}$, with $x_i \in \{0,1\}$ indicating whether site i , $i = 1, \dots, N$, is included in the solution or not. The value of a solution is the sum of the values V_j of the representations $R_j(\mathbf{X})$ of all species j , $j = 1, \dots, J$, in selection \mathbf{X} , depending on species weights, w_j , and targets, T_j . The constraint specifies that the summed cost of selected sites cannot exceed the resource available, C .

The important part of Eq. 1 is the definition of the value, V_j . We specify that

$$V_j(\mathbf{X}) = w_j f_j[R_j(\mathbf{X})], \quad (2)$$

where w_j is the weight and f_j is a benefit function for species j . Thus, we have two distinct components affecting the value of a certain species' representation in the network: (1) the species-specific weight, w_j , and (2) the benefit function, f_j . The term *benefit function* comes from economic ecology (e.g., Wu & Boggess 1999) and means that different levels of representation produce different benefits in terms of the perceived (nonmonetary) value of the reserve network. An analogous term is *utility function*, which is commonly used in a similar context in decision analysis or economics. Fundamentally, the use of benefit functions and species weights formulates the reserve selection problem as a multicriteria decision problem, with the weights and benefit functions defining tradeoffs between species representations.

For benefit functions, the commonly used form in reserve selection studies is the step function (I). We argue that the step function is unsatisfactory because it does not recognize how much above or below the target the species representation is. We propose using a benefit function in which value increases with representation,

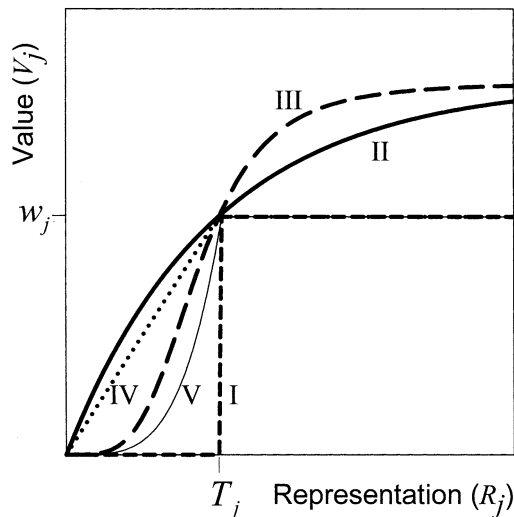


Figure 1. Alternative functional forms for benefit function f_j (I–V). The y-axis is the value of species representation, $V_j(R_j) = w_j f_j(R_j)$, which is affected by both the benefit function f_j and species weight w_j . The value of zero populations is zero ($f_j(0) = 0$), the value of the representation at a species-specific target level T_j ($f_j(T_j) = 1$) is equal to the species weight, and f_j is a nondecreasing function of R_j ($f_j'(R_j) \geq 0$), such that V_j either remains constant (threshold) or increases for $R_j > T_j$. Formulations and interpretations for these functions are in Table 1.

such as functions (II) and (III) (Fig. 1, Table 1); then, overrepresentation and underrepresentation with respect to the target become automatically valued. The choice of the benefit function should be carefully considered and ideally based on species biology (Table 1).

An important parameter in our formulation is r , which specifies what proportion of the maximum value $V_j(\mathbf{X})$ is achieved when $R_j(\mathbf{X}) = T_j$. Low r indicates that overrepresentation may increase the value of the solution significantly, and r close to 1 indicates that overrepresentation is given only minor value. Typically, one would use low r for rare or valuable species and high r for common species.

In addition to valuing over- and underrepresentation, we argue that the species should in many cases be given weights, w_j . We assigned weights to the species based on the following formula:

$$w_j = (pW_j^R + (1 - p)W_j^N)W_j^T, \quad (3)$$

where W_j^R , W_j^N , and W_j^T are weights for regional rarity, national rarity, and taxonomic value for species j , respectively, and $p \in [0,1]$ is a parameter defining the balance between the two rarity weightings.

We solved the optimization problems with the RSW software (Moilanen 2004), which uses forward and backward heuristics and simulated annealing for finding a near-optimal solution to Eq. 1.

Application of Formulation

We applied our approach to conservation of herb-rich forests in southern Finland. Of the sites described by Heikkinen (2002), we selected as our set of candidate sites 224 herb-rich forests located on continental Finland: 110 protected areas and 114 regionally valuable but unprotected forests. Lacking cost data, we used site area as a surrogate for cost. We used occurrence records of 75 vascular plant species characteristic of herb-rich forest in the site-selection analysis. Species included several Finnish Red Data Book species (Rassi et al. 2001) and rare species (as defined in Hämet-Ahti et al. 1998).

We chose two diverse benefit functions for our selection experiments. For plants, even small populations and reserves can be valuable (Lesica & Allendorf 1992; Turner & Corlett 1996). Thus we chose function (II) (Fig. 1) as the most realistic alternative. This function gives relatively high value at low levels of representation. As a comparison, we used the step imitation function (Fig. 1, function V), which approaches the standard practice in reserve-selection studies. We used a step imitation instead of a real step function because it can be used with the same (continuous function) optimization algorithm as functions II and III. The target level of representation, T_j , was set to five populations for all species (T_j plays a minor role because it is not a threshold target). The parameter r was set to 0.1 for all red-listed species, meaning that an abundant overrepresentation could cause up to a 10-fold increase

Table 1. Forms of benefit functions $f(R)$ (same indexing as in Fig. 1) for use in reserve-selection procedures.^a

No.	Function	Properties and usage
I	$f(R) = 0$ when $R < T$, $f(R) = 1$, when $R \geq T$	step function: zero value for underrepresentation, value is 1 for T and overrepresentation—species is “0/1 represented”; has been used almost exclusively in both maximum coverage and minimum set studies
II	$r^{-1}[1 - \exp(-\gamma R)]^b$ $f'(R) > 0$, $f''(R) < 0$	value keeps increasing with increasing representation but approaches an asymptote; relatively high value already at low levels of representation; marginal value of an additional population decreases with increasing representation, $f'(R) \leq 0$; use for species that are able to persist at low levels of representation (e.g., plants)
III	$r^{-1}[R^\beta/(R^\beta + \gamma)]^{b,c}$ $f'(R) > 0$, $f''(R) > 0$ for $R < T$, $f''(R) < 0$ for $R > T$	a sigmoid approaching an asymptote; low representation has low value; after T has been reached, marginal value of an additional population decreases with increasing representation; for species that have an extinction threshold at a known level below T (metapopulation species, probability of persistence low at low R), or for an economically important species to maintain a certain population size required for sustainable harvesting
IV	$f(R) = R/T$ when $R < T$, $f(R) = 1$ when $R \geq T$	value increases linearly until T is reached, then no increase; no particular assumptions on significance of underrepresentation, overrepresentation not valued (target, with valuing for underrepresentation)
V	$f(R) = (R/T)^\beta$, when $R < T$, $f(R) = 1$ when $R \geq T$, $\beta > 1$	some value for underrepresentation; created for computational convenience to approximate function I using a continuous function; used instead of the step function in the RSW program

^aThe value $V_j(R_i) = w_j f_j(R_i)$ and index j for species was dropped for convenience purposes.

^bParameter γ is determined so that the condition $f(T) = 1$ is satisfied for a given r . Fundamentally, γ is determined by T and r , but for simplicity we used γ to represent a more complicated factor, which is automatically calculated from T and r by the RSW software.

^cParameter β determines the steepness of the curve.

in the perceived value of that species. Of those that were not red listed, the species belonging to any regional rarity category were assigned an r value of 0.5 (hereafter referred to as rare species) and the rest of the species (common species) were assigned an r of 0.9.

Our regional rarity weights were based on the *Field Flora of Finland* (Hämet-Ahti et al. 1998) and varied from 1 to 4 depending on the regions in which the species was classified as rare. For national rarity we used red-list classifications (Rassi et al. 2001) ranging from 1 (not red listed) to 5 (critical). For taxonomic weights we used the root weight of May (1990) and Vane-Wright et al. (1991). For parameter p , defining the balance between W^R and W^N , we used 0.3 throughout the study. With this value species that were rare in the whole country had approximately equal weights to species classified as near threatened. The total weights (Eq. 3), w_j , varied from 1 to 12.07, with an average of 2.16. Our default weighting scheme consisted of these weights with benefit function (II) in Fig. 1.

Results

The effects of weighting species on the selection of herb-rich forest sites were measured as the proportion of the sites selected in our default weighting or value scheme, which was also selected using each of the other weighting or value schemes (similarity; Fig. 2). The benefit function was the critical part of our formulation (Fig. 2). The similarity between a weighted and unweighted ($w_j = 1$) function II at different resource levels was $> 85\%$. When the valuing of overrepresentation was changed so that it was

equal for all species, whether they were common or not ($r = 0.5$), the similarity to our default weighting scheme decreased to only 60–80%. This is not very surprising. Using equal r for all species makes it possible to increase the value of the solution by obtaining more occurrences for even the commonest species, whereas our default weighting allows significant value increase only via overrepresentation of rare species. Consequently, the optimal site selection changed. When species weights were removed, similarity decreased even further. The unweighted-step-imitation function (Fig. 1, function V) mimicks common practice in reserve selection. The largest differences were found between it and our default scheme. The similarity between solutions was only 40–60% for a wide range of resources. Furthermore, the difference was large even between function II and the weighted-step-imitation function, indicating that the use of a benefit function had a much greater effect on the optimal selection than the use of weights.

In our example, the step imitation function was less efficient than function II in obtaining representation for rare and red-listed species because overrepresentation was not valued (Fig. 3). There was a notable difference in representation of red-listed and rare species between the unweighted step function and weighted function II, and even without weights (but with varying r) function II resulted in comparatively higher representation levels for rare species. For our data, all the common species were covered already at low resource levels when rare and red-listed species were targeted. This indicates a nestedness of vascular plant taxa in northern European herb-rich forests.

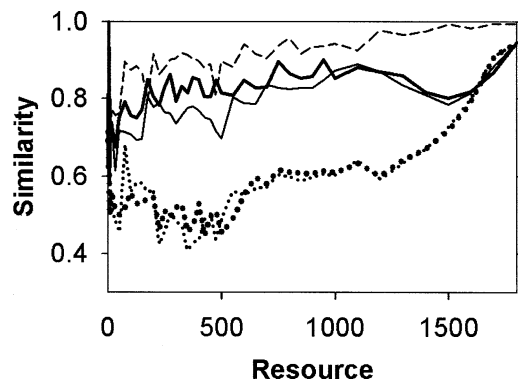


Figure 2. Effects of the use of species weighting and different benefit functions to selected sets of reserve sites at different resource levels. Sets of sites selected with different weighting schemes are compared with the default scheme [$w_j = (0.3 W^R + 0.7 W^N) W^T$ with function II] solution. Similarity is expressed as proportion of shared sites: a similarity of one indicates the same choice of localities, whereas lower values indicate different choices of sites. The dashed line represents function II without species weights (i.e., the difference is caused by species weights only). The thick solid line is the default scheme with the exception that all species have $r = 0.5$, increasing the value of overrepresentation for the common species and decreasing the value of overrepresentation for the rare species. The thin solid line represents function II with $r = 0.5$ for all species as above but without species weights. The thick dotted line is the step imitation function (function V, Fig. 1) with species weights, and the thin dotted line corresponds to the unweighted step function.

We also investigated the potential need for enlargement of the current (1337 ha) reserve network. The value of the existing network was only slightly suboptimal compared with what could be achieved with the same resource level

if reserve planning were started from scratch. We identified 19 sites (30 ha) that would significantly increase (from $F = 159$ to 166 in Eq. 1) the value of the conservation area via improved representation for 15 rare species.

Discussion

It appears reasonable that the value of biodiversity in a reserve network should increase with an increasing level of representation—more populations are better than fewer populations—and species that are present should have some value even if they fall below a particular target level. Reserve-selection formulations with fixed targets for representation do not operate in this manner. Also, rare, declining, or phylogenetically distinct species are likely to be more valuable, or require greater conservation efforts, than common species. Most previous complementarity-based studies of reserve selection, however, have not used species weights.

Use of a continuous benefit function with weights will have different consequences, depending on the data used. In our case all common species were covered (at a five-population level) even at a comparatively low resource level, and the effects of different weightings could be seen only in levels of representation between the different groups (red listed, rare, and common species) and in the dissimilarity between sets of selected sites. It is possible that more dramatic tradeoffs will result if the degree of nestedness of the taxa is lower. For example, a site that increases the representation of some endangered species might be preferred over a site that adds a new, but common species to the selection. Thus the number of species represented might be lower, but the probability of persistence would be higher for those species that are represented.

Our results show that weighting species and valuing varying levels of representation makes a great deal of difference in reserve selection, and we suggest that they

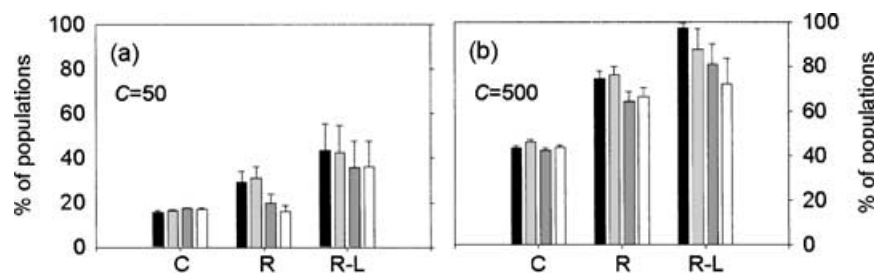


Figure 3. The effects of the different weighting schemes on the average levels of representation for species in different rarity classes: C, common; R, rare; R-L, red-listed, expressed as the mean percentage (+1SE) of populations represented for the species in each class. The resource level (C) is 50 ha in (a) and 500 ha in (b). Bars represent, from left to right: the default weighting, the unweighted function II, the weighted step imitation function (function V), and the unweighted step imitation function.

result in an improved reserve network compared with typical selection procedures that rely on the step function. In our empirical case the difference between the default weighting scheme (using weights and benefit functions) and an unweighted step function imitation could be more than 50%, as measured by the percent similarity of optimal selections. Furthermore, the greatest differences in representation of rare and red-listed species can be seen between the same two scenarios: the default scheme protected a much higher percentage of rare and red-listed species' populations. The default scheme corresponds to what we considered a reasonable choice from among the infinite number of alternative weightings and benefit functions. The unweighted-step-imitation function corresponds to what is actually being done in most complementarity-based reserve selection studies. This suggests that it is of primary importance to consider the effects of weighting and valuing of species representation in reserve selection.

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